THE GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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ROSACEAE A. L. de Jussieu, Gen. Pl. 334. 1789, nom. cons.

(ROSE FAMILY)

Trees, shrubs, perennial herbs, or, infrequently, annuals, sometimes armed with thorns or prickles; indumentum of simple and/or stellate or glandular trichomes; plants often increasing vegetatively by rhizomes, runners, creeping stems, or suckers. Leaves alternate [very rarely opposite], simple to palmately or pinnately compound, cauline and/or basal, sometimes clustered on short shoots, short to long petiolate, the blades commonly toothed and lobed; stomata ranunculaceous; stipules present (absent in some Spiraeoideae), paired, inconspicuous to foliaceous, often adnate to the petioles. Inflorescences terminal or axillary cymes, corymbs, umbels, racemes, spikes, or panicles, infrequently reduced to a single flower; bracts subtending the inflorescences and their branches. Flowers perfect, rarely imperfect and the plants then dioecious or monoecious, regular or rarely slightly irregular by displacement, 5-merous (or rarely 4-merous), the insertion of the perianth and androecium perigynous to epigynous, seldom nearly hypogenous. Calyx lobes 5 (rarely 4), often with an equal number of alternating epicalyx lobes, appearing to arise from the rim of the floral cup, nearly always persistent in fruit, valvate (quincuncial in *Rosa*) in aestivation; floral tube (cup) various: flat, cup-shaped, cylindric, campanulate, turbinate, or urceolate, free from or adnate to the carpels, often enlarging in fruit, a nectar ring usually inside the rim of the cup or lining it. Petals the same number as the calyx lobes, rarely absent or "doubled," white, yellow, pink, purple, or orange, never

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This paper has been scrutinized by Professor Wood, and I am most grateful for his numerous suggestions and corrections. Appreciation is also extended to Nancy Dunkly and Judi Hanhisalo for checking many of the references and typing parts of the manuscript. The illustrations of *Aruncus*, *Porteranthus*, *Fragaria* and *Duchesnea*, *Potentilla*, *Prunus*, *Pyrus* subg. *Aronia*, and *Rosa* are by Karen Stoutsenberger Velmure; those of *Neviusia* and *Physocarpus* by Rachel A. Wheeler; that of *Amelanchier* by Arnold D. Clapman.

blue or truly red, often shortly clawed below, caducous, imbricate or rarely contorted in bud, inserted at the upper edge of the floral cup. Androecium most frequently of 15 or more centripetally developing stamens in several series (whorls) with the inner ones shorter than the outer, or often 10 (8) in one series, or infrequently 5 (4), or rarely reduced to 1 or 2, inserted on the rim of, or rarely on the adaxial wall of, the floral cup; filaments free or basally united to the nectar ring, commonly persistent; anthers small, ± versatile (or infrequently basifixed), 2-loculate at anthesis, dehiscing introrsely [or extrorsely] by longitudinal slits [very rarely by subterminal pores], the locules sometimes separated by broad connectives; pollen 2-celled when shed, basically tricolporate, the sexine striate. Gynoecium of 1 to many spirally or cyclically arranged carpels inserted at the base of, on the sides of, or inclosed by the floral cup, the receptacle flat, concave, or convex to hemispheric or cylindric, the carpels or receptacles infrequently stipitate, the carpels apocarpous [rarely syncarpous], although sometimes ± laterally connate and abaxially adnate to the floral cup, the ovaries superior to partly or completely inferior; styles as many as the carpels, free or connate below, terminal, lateral, or nearly basal, deciduous or persistent; stigmas terminal, punctiform, discoid, or in bands decurrent on the styles; each carpel with 1 or 2 (or more in the Spiraeoideae) anatropous (rarely orthotropous) ovules basal, lateral, or pendulous from the adaxial wall, the micropyles abaxial. Fruits very diverse: follicles (sometimes dehiscing along both adaxial and abaxial sutures), achenes exposed or inclosed within the floral cup, pomes, drupes, or aggregate or accessory with drupelets or achenes [or very rarely capsules]. Seeds very small to large, variously textured [winged in tribe Quillajeae]; endosperm usually absent or sparse (abundant in some Spiraeoideae); embryo spathulate, the cotyledons fleshy, plano-convex [rarely foliaceous, convolute, or folded], the radicle straight to slightly bent, superior or inferior. Base chromosome numbers 7, 8, or 9. (Including Spiraeaceae D. Don, Malaceae J. K. Small, and Amgydalaceae D. Don; excluding Chrysobalanaceae R. Brown [see Prance]). TYPE GENUS: *Rosa* L.

About 100 genera and 3000 species (not including "microspecies" of apomictic genera) in four subfamilies and 13 tribes. Members of the family can be found in nearly every region of the world where vascular plants occur, but Rosaceae are most abundant, both in numbers of individuals and of diverse forms, in the North Temperate regions, particularly western North America and eastern Asia. No genus is restricted to Europe and no tribe to the Old World; tribe Quillajeae is limited to the New World. With the exception of the Kerrieae (Rosoideae), all tribes are represented in western North America. Twenty-two genera (three introduced from the Old World) of all four subfamilies and 10 tribes occur in the southeastern United States; an additional eight genera (including five that have escaped from cultivation) are found in northeastern North America. *Porteranthus*, *Neviusia*, and *Dalibarda* are endemics of

eastern North America. Twenty-three more genera grow in western North America, and of these 20 (or 21 if *Heteromeles* is considered distinct from *Photinia*) are essentially restricted to that area. Five genera (six if *Hesperomeles* is separated from *Osteomeles*) do not occur outside of Central and South America. Forty-five genera have species indigenous to North America, and there are 42 with species restricted to that region.

Although diverse in vegetative and fruit morphology, the family is a natural one. There has long been rather general agreement about the supraspecific taxa that are related to one another, but the taxonomic rank given these groups varies greatly. Perhaps as few as 80 or as many as 130 genera can be recognized. The genera, in turn, have been grouped variously into subtribes, tribes, or subfamilies, and several tribes and/or subfamilies are often given familial status. The information available at present indicates that *Chrysobalanus* and its relatives should be considered as a separate family, Chrysobalanaceae (see Prance), and that *Neurada*, *Neuradopsis*, and *Grielum* are best segregated as Neuradaceae. The remaining genera of Rosaceae can be assigned to four subfamilies: Spiraeoideae (with tribes Neillieae, Spiraeeae, Sorbarieae, Quillajeae, and Exochordeae), Rosoideae (with tribes Kerrieae, Fragarieae, Dryadeae, Ulmarieae, Sanguisorbeae, Adenostomateae, Roseae, and Rubeae), Amygdaloideae, and Maloideae. On the basis of morphological, cytological, and chemical data, it seems that Spiraeoideae and Amygdaloideae are the basic stocks of the family, the Rosoideae being derived from the Spiraeoideae by reduction in the number of ovules per carpel with a concomitant increase in the number of carpels per flower (the fruits becoming indehiscent), a dramatic multiplication or reduction in the number of stamens in many cases, a decrease in the base chromosome number, the loss of flavonols and sorbitol, and the acquisition of ellagic acid. Maloideae perhaps arose through hybridization between some ancient species of Spiraeoideae and Amygdaloideae (see discussion under Maloideae).

In the Englerian scheme of classification, Rosaceae are placed along with Platanaceae, Crossosomataceae, Connaraceae, and Leguminosae in suborder Rosineae of the Rosales. Most recent phylogenists group Platanaceae with Hamamelidaceae and Crossosomataceae with Dilleniaceae, and there is rather general agreement that Rosaceae, Saxifragaceae, Leguminosae, and Connaraceae are allied, although various taxonomic ranks are recognized. Hutchinson included Dichapetalaceae and Calycanthaceae in his Rosales.

Flowers of Rosaceae vary greatly in size, from very small, as in species of *Alchemilla*, *Aruncus*, and *Spiraea*, to large and showy, as in *Rosa* and *Rubus*. Flower color ranges from white and cream to yellow, pink, purple or orange; blues are totally absent (see below), and true red flowers occur rarely, if ever. Rosaceae do not seem to have undergone a series of extensive adaptations related to different pollination mechanisms such as those found in Ranunculaceae. Most species of Rosaceae have rather generalized perfect, regular, flat or shallowly cup-shaped flowers with a prominent nectar ring at the apex of the floral cup. Flies and short-

tongued bees are the commonest pollinators of small flowers, while long-tongued bees, other Hymenoptera, Coleoptera, and Lepidoptera visit large-flowered species. Some species of *Sanguisorba* lack petals and are wind pollinated. Homogamy and, to a lesser extent, proterogyny are common in the family. Should cross pollination not take place, many species are automatically self pollinated and are self compatible. Imperfect flowers regularly occur in some species of *Aruncus*, *Bencomia*, *Cliffortia*, *Dryas*, *Hagenia*, *Kageneckia*, *Osmaronia*, *Rubus*, and *Sanguisorba*, and the plants are then dioecious or variously monoecious.

Many fruit types occur in Rosaceae, and fruit morphology is used as a prime character in the subdivision of the family. The fruits of most Spiraeoideae are follicles (legumes?) that may split along both adaxial and abaxial sutures. *Holodiscus* is the only member of the Spiraeoideae with achenes. In *Exochorda* the carpels become connate at maturity, and the fruit is capsular. *Lindleya* and *Vauquelinia* have loculicidal capsules. Rosoideae have achenes or drupelets, these sometimes aggregated, or inclosed by the dry to fleshy floral cup, or borne on the fleshy receptacle. All Maloideae have pomes (see discussion under that subfamily), while drupes are produced by members of the Amygdaloideae.

The family seems to have undergone an extensive series of adaptations evidently tied to dispersal by various means. Mechanisms for dispersal by wind are found in tribe Quillajeae (winged seeds), some Spiraeoideae (small seeds with loose, membranaceous seed coats), many Dryadeae (plumose styles), and some Sanguisorbeae (winged floral cups that inclose the seeds). Adaptations for transport by attachment to animals are found in Dryadeae (hooked styles), some species of *Rosa* (prickles on the floral cups), and some Sanguisorbeae (hooked bristles or spines with retrorse barbs on the floral cups). Certain species of *Potentilla* that have achenes with elaiosomes are dispersed by ants. Many Rosaceae have fleshy fruits and are eaten by mammals, birds, and reptiles, the seeds passing through the digestive tracts. In *Prunus* and *Rubus*, the outer carpel walls become fleshy, in *Fragaria* and *Duchesnea*, the receptacles, and in *Rosa* and all Maloideae, the floral cups.

Chromosome numbers have been reported from species representing over 60 genera. Unfortunately, many of these counts are old, undocumented, and/or from cultivated materials of unknown origin, and some widespread genera, as well as some commonly cultivated (at least in botanical gardens), have not been examined cytologically. A concentrated effort to obtain counts for as many Rosaceae as possible would be most worthwhile, even if tedious. Subfamily Spiraeoideae has a base chromosome number of 9, with only a few occurrences of 8 or 10. *Quillaja brasiliensis* is anomalous in that it is thus far the only known species of Rosaceae outside the subfamily Maloideae with a chromosome number $2n = 34$. Except for some populations of *Aruncus dioicus*, only diploids and tetraploids occur in Spiraeoideae. Subfamily Rosoideae has base numbers of 7 and 9, rarely 8. A base number of 9 occurs mostly in tribes Kerrieae, Adenostomateae, and some New World genera of Dryadeae.

Many genera of Rosoideae have polyploid series, and the highest chromosome number known for the family is $2n=$ ca. 224 in *Alchemilla faroënsis*. The base chromosome number of subfamily Amygdaloideae is 8, and most species are either diploid or tetraploid. All members of subfamily Maloideae have a base number of 17; see the discussion under that subfamily for several hypotheses on the possible origin of this number.

Many Rosaceae have been rather extensively studied for their chemical constituents, especially phenolics. Cyanidin is the common petal pigment, with pelargonidin rarely occurring; delphinidin is absent (hence no blue-flowered Rosaceae). Leucocyanidin occurs in the leaves of all species; leucodelphinidin is known only from *Potentilla anserina* (but it regularly occurs in Chrysobalanaceae). The flavonols kaempferol and quercetin are ubiquitous, while the family (with the exception of *Potentilla anserina*) lacks trihydroxy flavonoid compounds that are found in Chrysobalanaceae. Dihydrochalkones have been isolated from species of *Malus* and *Docynia* (Maloideae), *Adenostoma* (Rosoideae), and *Sorbaria* (Spiraeoideae). Flavone glycosides are present in all four subfamilies, but in Rosoideae are restricted to tribe Kerrieae. Ellagic acid is found in all Rosoideae, except the Kerrieae, but is lacking in the other subfamilies. Sorbitol occurs throughout the Maloideae, Amygdaloideae, Spiraeoideae, and tribe Kerrieae of the Rosoideae; it is absent from other Rosoideae. Arbutin is known from *Sorbaria* and *Exochorda* (Spiraeoideae), *Adenostoma* (Rosoideae), and *Pyrus* (Maloideae). Alkaloids seem to occur only rarely in the family.

Some members of Rosaceae are often confused with Ranunculaceae and Saxifragaceae. Rosaceae can be distinguished from the former by the flowers with floral cups, by the perigynous to epigynous insertion of the petals and stamens, and by the whorled stamens. Rosaceae differ from Saxifragaceae by the mostly alternate, stipulate leaves, the apocarpous gynoecium, and the more numerous stamens and carpels. Fruits of Rosaceae are diverse but are never berries as in some Ranunculaceae and Saxifragaceae, or are very rarely capsules as in most Saxifragaceae; seeds of Rosaceae lack endosperm (except for some Spiraeoideae).

Rosaceae are among the more economically important families of plants. Although no species is a staple food item, the diets of many peoples of the world are enriched by fruits of Rosaceae. From species of *Pyrus* come pears and apples; from *Prunus*, plums, cherries, peaches, nectarines, apricots, and almonds; from *Rubus*, blackberries and raspberries; from *Fragaria*, strawberries; from *Eriobotrya*, loquats; from *Amelanchier*, service berries; from *Cydonia*, quinces; from *Mespilus*, medlars; and from *Rosa*, rose hips. Rosaceae with fleshy fruits are important wildlife foods, and the foliage of *Purshia* and *Cowania* is eaten by game and livestock in southwestern North America. Many species of Rosaceae are used in home medicines for a variety of ailments; this is unusual for a family in which alkaloids are rare. Otto (or attar) of roses, an essential oil used in perfumery, is distilled from the petals of *Rosa*

Damascena. Wood from species of *Prunus*, *Pyrus*, *Crataegus*, and *Amelanchier* goes into the manufacture of furniture, musical instruments, and other items. Most genera of Rosaceae are cultivated to a limited degree, with *Crataegus*, *Prunus*, *Pyracantha*, *Pyrus*, *Rosa*, and *Spiraea* furnishing important ornamental plants in the Northern Hemisphere. Several states have designated members of Rosaceae as their state flowers or trees.

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KEY TO THE SUBFAMILIES, TRIBES, AND GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES

A. Gynoecium of 2 to many carpels (rarely one); fruit a follicle, pome, or achene, or fruit aggregate or accessory with drupelets or achenes; insertion perigynous to epigynous, the ovaries superior to inferior; ovules various; styles terminal to nearly basal.

B. Carpels free from the floral cup, although sometimes surrounded by it, the ovaries superior; fruits follicles, achenes, or drupelets; shrubs or herbs, unarmed or with prickles.

C. Fruits follicles, sometimes opening on both abaxial and adaxial sutures; ovules 2 or more per carpel; endosperm often present; stipules sometimes absent (subfam. SPIRAEOIDEAE).

D. Seed coat hard, shining; fruits inflated; endosperm abundant; carpels united at least basally; stipules present (NEILLIEAE). . . . . 1. *Physocarpus*.

D. Seed coat membranaceous or roughened, not hard and shiny; fruits not inflated; endosperm sparse or abundant; carpels free or basally united; stipules present or absent.

E. Stipules absent; carpels antepetalous, when 5; seeds small, tapering at each end, the coat membranaceous; endosperm sparse (SPIRAEEAE).

F. Plants shrubs; leaves simple; flowers perfect; carpels 5. . . . . 2. *Spiraea*.

F. Plants herbaceous; leaves several times pinnately compound;

flowers mostly imperfect, the plants dioecious; carpels usually 3(2–5). ..... 3. *Aruncus.*

E. Stipules prominent, persistent; carpels 5, antesepalous; seeds about 5 mm. long, not tapering, the coat hard, roughened; endosperm thick, fleshy (SORBARIEAE). ..... 4. *Porteranthus.*

C. Fruits indehiscent, a solitary achene or aggregate or accessory with several to numerous drupelets or achenes; ovules 1 or 2 per carpel; endosperm nearly always absent; stipules present, infrequently caducous (subfam. ROSOIDEAE).

G. Carpels several to many, becoming achenes or drupelets on a dry to fleshy receptacle; floral cup short, not inclosing the fruits.

H. Receptacle flat, with 4–10 carpels in one whorl; fruits large 1-seeded achenes.

I. Plants shrubs with simple leaves; flowers large; carpels usually 4 or 5 (KERRIEAE).

J. Leaves opposite; flowers 4-merous; petals white. ..... [*Rhodotypos.*]

J. Leaves alternate; flowers 5-merous.

K. Petals absent; flowers in few-flowered corymbs; calyx lobes large, foliaceous, deeply toothed. ..... 5. *Neviusia.*

K. Petals present, yellow; flowers solitary; calyx lobes short, entire. ..... [*Kerria.*]

I. Plants perennial herbs with pinnately compound leaves; flowers small; carpels 5–15 (ULMARIEAE). ..... 6. *Filipendula.*

H. Receptacle convex, with many carpels in several series (rarely 5–10, the plants then with both petaliferous and apetalous flowers); fruits small achenes or drupelets, in some aggregate or accessory.

L. Plants shrubs with or without prickles, rarely woody vines or perennial herbs; leaves of the herbaceous forms palmately veined and cordate at base; fruits aggregate, of fleshy or rarely dryish, 1-seeded drupelets; each carpel with 2 ovules; calyx ebracteate (RUBEAE).

M. Plants shrubs with erect, arching, or trailing stems; leaves compound or simple and palmately lobed; carpels numerous, becoming juicy drupelets; flowers petaliferous. ..... 7. *Rubus.*

M. Plants low, creeping evergreen, perennial herbs; leaves simple, with crenate margins and cordate bases; carpels 5–10, becoming achene-like drupelets; flowers of 2 types, petaliferous and apetalous. ..... 8. *Dalibarda.*

L. Perennial herbs with pinnately or palmately compound leaves; fruits small achenes; carpels with one ovule; calyx usually with an epicalyx.

N. Styles basal to subterminal, deciduous, or if persistent, the insertion lateral, not geniculate or plumose above; ovules anatropous and pendulous, ascending, or descending; receptacle dry or fleshy in fruit (FRAGARIEAE).

O. Receptacle enlarging, red and fleshy in fruit; leaves trifoliolate.

P. Flowers white; epicalyx lobes entire; mature receptacle juicy, flavorful; styles persistent. ..... 9. *Fragaria.*

P. Flowers yellow; epicalyx lobes apically 3–5 toothed; mature receptacles spongy, insipid; styles deciduous. ..... 10. *Duchesnea.*

O. Receptacle not enlarging, dry; leaves digitate, trifoliolate, or imparipinnate. ..... 11. *Potentilla.*

N. Styles terminal, wholly deciduous and terete or at least the lower part persistent and the upper part geniculate or plumose; ovules basal and upright-apotropous; receptacle dry in fruit (DRYADEAE).

Q. Styles geniculate or plumose above, at least the lower part persistent in fruit; lower leaves imparipinnate (rarely appearing simple). ..... 12. *Geum.*

Q. Styles straight, deciduous at base; leaves trifoliolate. ..... 13. *Waldsteinia.*

G. Carpels 1 to many, becoming achenes inclosed by the dry or fleshy floral cup.

R. Plants herbaceous; petals small or absent; carpels 1–4; floral cup dry in fruit (SANGUISORBEAE).

S. Floral cup armed with hooked bristles; petals present; leaves imparipinnate with large leaflets interspersed with smaller ones. ..... 14. *Agrimonia.*

S. Floral cup not armed; petals absent; leaves simple or imparipinnate with ± equal leaflets.

T. Plants tiny annuals; leaves simple, palmately lobed or dissected; stamen one; flowers perfect, in few-flowered sessile cymules. ..... 15. *Alchemilla.*

T. Plants perennials or moderate-sized, erect annuals; leaves imparipinnate; stamens 4–12; flowers often imperfect, crowded in dense heads or spikes at the tips of long peduncles. ..... 16. *Sanguisorba.*

R. Plants shrubs with prickles; flowers showy; carpels usually numerous, lining the base or sides of the fleshy floral cup (ROSEAE). ..... 17. *Rosa.*

B. Carpels surrounded by and adnate to the floral cup, the ovaries partly to completely inferior; fruit a pome; shrubs or trees, often armed with thorns (subfam. MALOIDEAE).

U. Endocarps becoming hard in fruit, the pomes usually with 5 stones (endocarps); thorns commonly numerous.

V. Shrubs with crenate-margined leaves; stipules caducous; stones often 2-seeded. ..... 18. *Pyracantha.*

V. Shrubs or trees with lobed and/or toothed leaves; stipules persistent; stones 1-seeded. ..... 19. *Crataegus.*

U. Endocarps becoming cartilaginous, membranaceous, or leathery in fruit, the pomes with 5–10 seeds; unarmed or rarely with a few thorns.

W. Flowers in rather elongated racemes; petals obovate to lanceolate, not clawed; pomes juicy, berry-like, appearing to be 10-locular; leaves serrate-margined or rarely entire. ..... 20. *Amelanchier.*

W. Flowers in umbel-like racemes or few- to many-flowered corymbs;

petals subcircular, clawed; pomes fleshy, 5-locular; leaves toothed and often lobed, or pinnately compound. ..... 21. *Pyrus*.

A. Gynoecium of one carpel; fruit a drupe; insertion perigynous, the ovaries superior; ovules 2, pendulous; styles terminal (subfam. AMYGDALOIDEAE). ..... 22. *Prunus*.

Subfam. SPIRAEOIDEAE Endlicher, "Subordo Spiraeaceae"

About 20 genera in five tribes; in our area four genera representing three tribes. Most genera of Spiraeoideae are small and of limited geographical distribution; only *Physocarpus*, *Spiraea*, and *Aruncus* occur in both the Old and New worlds. *Spiraea* is the largest genus with about 50 species. None of the other genera exceeds 15 species, and eight are either monotypic or have only two species. *Porteranthus* is endemic to eastern North America, seven genera are confined to western North America, two are South American, and six are Asiatic. The two tribes that do not occur in the southeastern United States are Quillajeae, with *Quillaja* Molina (3–6 spp. of South America), *Kageneckia* Ruiz & Pavon (3–6 spp. of temperate South America), and *Vauquelinia* Corrêa ex HBK. (8–10 spp. of the southwestern United States and Mexico); and Exochordeae, with *Exochorda* Lindley (about 5 spp. of central and eastern Asia) and *Lindleya* HBK. (2 spp. of Mexico). The relationships of *Holodiscus* (K. Koch) Maxim. (about 6 spp., British Columbia to Bolivia) are unclear; the genus has been placed in the Spiraeeae, in a distinct tribe of Spiraeoideae or Rosoideae, or considered to be transitional between the two subfamilies. *Lyonothamnus floribundus* Gray, $2n = 54$, of four offshore islands of southern California, has been included in tribes Sorbarieae and Quillajeae.

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Tribe NEILLIEAE Maximowicz

1. **Physocarpus** (Cambessèdes) Rafinesque, New Fl. N. Am. 3: 73. 1838 (Jan.-Mar.), "*Physocarpa*"; corr. Maximowicz, Acta Horti Petrop. 6: 219. 1879, nom. cons.[2]

[2] *Epicostorus* Rafinesque (Atlantic Jour. 1: 144. 1832; type species *E. montanus* Raf. = *Physocarpus monogynus* (Torrey) Coulter) is earlier than *Physocarpus* (Camb.) Raf. When the two genera are united, as in current practice, *Epicostorus* would be the correct name, even though *Physocarpus* is conserved. In the interest of nomenclatural stability, it has been proposed that *Epicostorus* Raf. be added to the

Deciduous shrubs with erect or spreading principal branches and terete or slightly 5-angled short lateral branches; bark in several layers, the outer peeling off in longitudinal strips; buds small, solitary, sessile; indumentum of stellate trichomes, very variable in density. Leaves simple, alternate, distinctly petiolate; blades dentate, palmately 3–5-lobed, with the center lobe usually larger than the lateral ones, the blades of vegetative branches longer and more strongly divided than those of flowering branches, the blades of immature leaves often unlobed; leaf scars elevated, semielliptic and ± 3-lobed with 5 bundle traces; stipules linear, deciduous. Inflorescences many-flowered, bracteate, umbel-like corymbs [panicles, or racemes] terminating lateral branches of the current year. Calyx ebracteolate, the 5 lobes spreading to reflexed, persistent, valvate in aestivation; floral cup hemispheric, free of the carpels. Petals 5, white to pinkish, spreading, deciduous, suborbicular, perigynous at the edge of the floral cup. Androecium of 20–40 exserted stamens; filaments long, filiform, equal [or alternate filaments shorter], arising from a nectar ring that surrounds the mouth of the floral cup, some persistent; anthers small. Gynoecium of 3–5 [1], shortly stipitate carpels, antepetalous when 5, united at the bases [or for more than half their length]; styles terminal, elongated, the lower part persistent as a beak on the fruit; stigmas subcapitate; each carpel with 2–4 superposed ovules on an adaxial placenta, the upper ascending, with the micropyle inferior, the lower pendulous, with the micropyle superior. Fruits firm-walled, ± inflated, few-seeded follicles, often dehiscent along both adaxial and abaxial sutures. Seeds obliquely pyriform, the seed coat hard, shining; endosperm copious; embryo spatulate, the cotyledons plano-convex, the radicle inferior or superior. Base chromosome number 9. (*Spiraea* sect. *Physocarpos* Camb., *Opulaster* Medicus ex Schneider; including *Epicostorus* Raf.) TYPE SPECIES: *Spiraea opulifolia* L. = *P. opulifolius* (L.) Raf.[3] (Name from Greek, *physa*, a bladder or pair of bellows, and *karpos*, a fruit, in refer- to the inflated follicles.) — NINEBARK.

Six or more species with an Arcto-Tertiary distribution: *Physocarpus opulifolius* (L.) Raf. in eastern North America, about four species in the Cordillera of western North America, and *P. amurensis* Maxim. in Manchuria and Korea. Most species occur in moist, rocky habitats in foothills or mountains.

Although five species (three supposedly endemic) have been reported from our area, there appears to be only a single, more or less polymorphic species, *Physocarpus opulifolius*, $2n = 18$, that ranges from extreme northern Florida and adjacent Georgia, northward to Maine, Nova Scotia, and

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nomina generica rejicienda as a taxonomic synonym of *Physocarpus* (Taxon **21**: 211, 212. 1972), and this proposal has been approved by the Committee for Spermatophyta (Taxon **22**: 156. 1973).

[3] Abrams (Illus. Fl. Pacific States **2**: 409. 1944) incorrectly gives the type species as *P. amurensis* Maxim.; lectotypification is unnecessary, since *S. opulifolia* L. was the only species referred by Cambessèdes to his section *Physocarpos*.

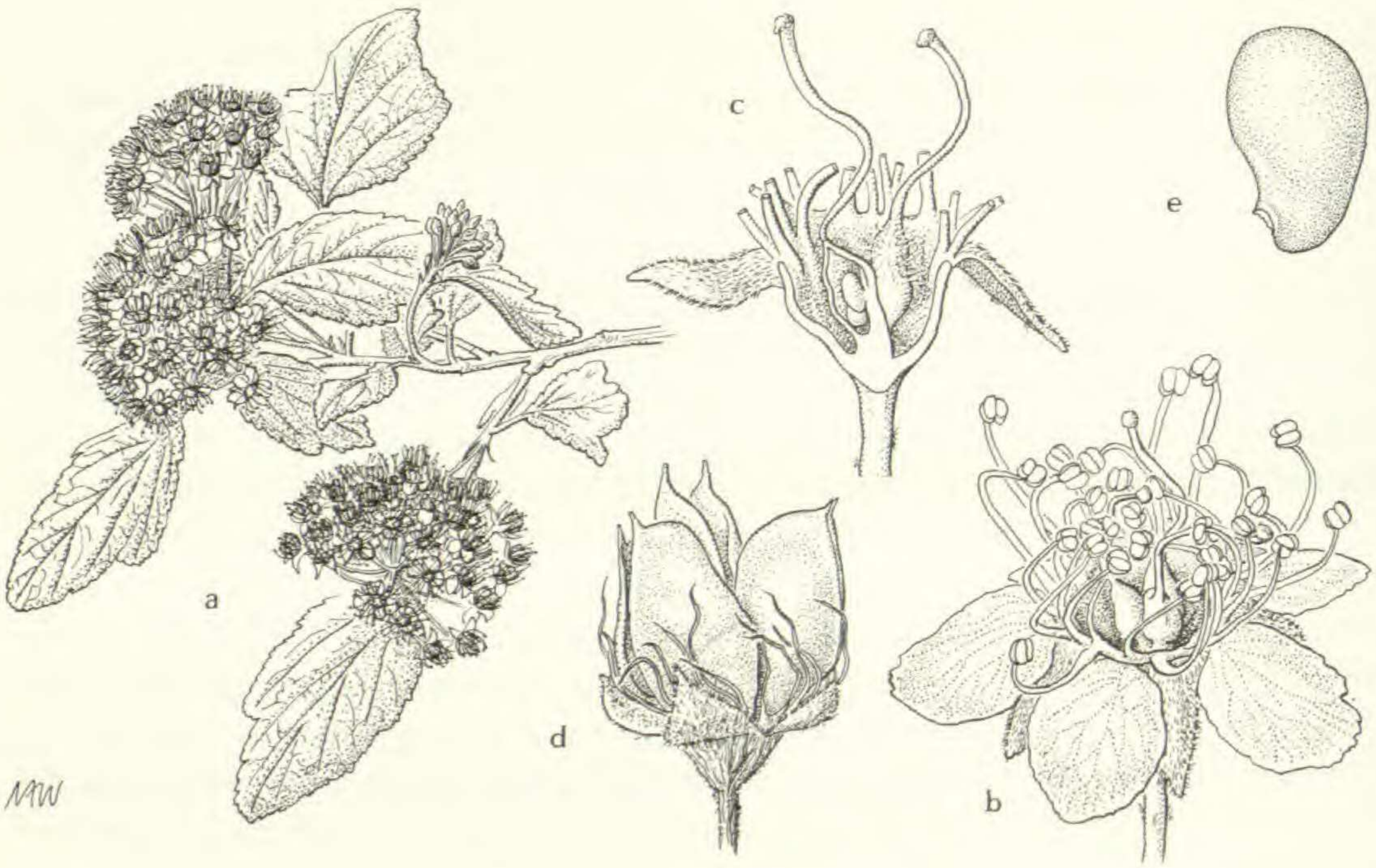

FIGURE 1. **Physocarpus.** a–e, *P. opulifolius*: a, flowering branchlet, × 1/2; b, flower, the stamens (not fully expanded) inserted on nectar ring, × 5; c, flower in vertical section to show placentation and floral cup, most of staminal filaments removed, × 6; d, mature fruit after dehiscence, the follicles open, × 3; e, seed, × 12.

James Bay, westward to Arkansas, southeastern Kansas, Missouri, Iowa, and Minnesota, and that also occurs disjunctly in the Black Hills of South Dakota and in central Colorado. This species is particularly variable in indumentum density and persistence, and certain variations are to some degree geographically restricted. Almost glabrous plants are most common in the northeastern United States and adjacent Canada and occur west to Minnesota and south to Georgia but are absent in the Midwest. Plants with pubescent pedicels and sepals and glabrous follicles are the commonest form in most of the eastern United States. Toward the Midwest and South, pubescence of leaves, young branches, pedicels, sepals, and follicles increases in density. Plants with varying degrees of pubescence have been segregated as *P. intermedius* (Rydb.) Schneider (*P. opulifolius* var. *intermedius* (Rydb.) Robinson = ? var. *tomentellus* (Seringe ex DC.) Boivin), *Opulaster alabamensis* Rydb., and *P. stellatus* (Rydb.) Rehder. The mature follicles are variable in shape and size; Rydberg distinguished those plants with small, abruptly acute follicles as *Opulaster australis* (*P. australis* (Rydb.) Rehder).

Characteristic plants of *Physocarpus opulifolius* in the eastern United States have obtuse to acute or rarely acuminate leaf dentation (leaves of the vegetative branches generally have sharper teeth than those of the flowering stems). Toward the west, and to some degree toward the south, the teeth are more acute or (commonly) acuminate. All Twentieth

Century floras and treatments of the genus recognize as distinct the western *P. capitatus* (Pursh) Kuntze (southern Alaska to coastal southern California; mostly west of the Cascade Mountains, but disjunct in northern Idaho), $2n = 18$, which differs from *P. opulifolius* in the consistently acute or acuminate leaf toothing and slightly larger flowers, follicles, and seeds. The Asian *P. amurensis* also differs from *P. opulifolius* by virtually the same characteristics. It needs to be ascertained whether these three taxa are actually conspecific. Evidently much could be learned from biometric studies of the variations found in species of *Physocarpus*.

Other generic names have been applied to this genus. *Physocarpus* was considered by Bentham & Hooker to be congeneric with *Neillia*, and this interpretation was followed by both Greene and Jones. Today however, these two genera are recognized as distinct. *Opulaster* Medicus (Pfl. Anat. 109. 1799) was adopted by Schneider and by Rydberg and used in several subsequent floras, but this name was a nomen nudum that was validated by Schneider. In addition to *Physocarpus*, Rafinesque published two other generic names that involve this genus, *Icotorus* (Bull. Bot. Seringe 1: 216. 1830), a nomen nudum, and *Epicostorus* (see footnote 2).

The genus is separable into two more or less distinct groups. *Physocarpus opulifolius*, *P. capitatus*, and *P. amurensis* comprise one group with the carpels usually numbering three to five (rarely fewer) and united only at the bases. Members of the other group, including *P. alternans* (M. E. Jones) J. T. Howell, *P. monogynus* (Torrey) Coulter, and *P. malvaceus* (Greene) Kuntze, all of western North America, have either solitary carpels or two (rarely to five) carpels united at least half their lengths. The species in both groups are variable and sometimes difficult to distinguish; numerous segregate species have been proposed.

Physocarpus, *Neillia* D. Don (10 to 13 species of the Himalayas to eastern Asia and Java and Sumatra), and *Stephanandra* Sieb. & Zucc. (4 or 5 species of eastern Asia) comprise the tribe Neillieae, characterized by the presence of stipules, carpels (when more than one) united at least basally, hard and shining seed coats, and abundant endosperm. Hutchinson included *Guamatela* Donn. Sm. (monotypic; Guatemala) in this tribe, although it differs from the other three genera in the free carpels and absence of endosperm.

Species of *Physocarpus* are cultivated as ornamentals under the name "Ninebark," in reference to the layered, peeling bark, and there are several named cultivars of *P. opulifolius*. The plants are attractive, although not very showy, and are grown primarily in botanic gardens, in parks, and on campuses. *Physocarpus opulifolius* has become naturalized in parts of Europe.

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Tribe SPIRAEEAE Jussieu [4]

2. **Spiraea** Linnaeus, Sp. Pl. 1: 489. 1753; Gen. Pl. ed. 5. 216. 1754.

Deciduous shrubs with numerous erect, reclining, or ascending stems, mostly unbranched below the inflorescence to diffusely branched; branches terete, sometimes angled from the nodes, with a small, round, continuous pith; buds small, solitary [or collaterally multiplied], sessile, with 2–8 exposed scales; indumentum of simple trichomes, variable in density. Leaves simple, alternate, shortly petiolate to subsessile; blades ovate, elliptic, or obovate with dentate, entire [or lobed] margins; leaf scars minute, strongly elevated, semicircular or crescent shaped with 1 bundle trace; stipules generally absent. Inflorescences many-flowered, bracteate, compact panicles, compound [or simple] corymbs [racemes or umbels] terminal on branches of the current year [or lateral from buds of the preceding year's growth]. Flowers small, perfect [rarely imperfect, the plants polygamous]. Calyx ebracteolate, the 5 lobes short, triangular, erect or spreading, deciduous in fruit or persistent, valvate or slightly imbricate in aestivation; floral cup hemispheric, campanulate, or turbinate, free from the carpels. Petals white to rose, widely spreading, equal, suborbicular to obovate with slightly undulate or uneven margins, very shortly clawed, deciduous, imbricate or contorted, inserted at the outer edge of the nectar ring. Androecium of 15 to many exserted stamens; filaments slender, unequal in length, free except at the base, inserted in one to several series at the edge of the floral cup between the perianth and a usually prominent, fleshy nectar ring that surrounds the mouth of the floral cup. Gynoecium usually of 5, free, antepetalous, superior carpels; styles terminal or subterminal, elongated, forming a beak on the fruit; stigmas capitate-discoid; each carpel with 2 to several anatropous ovules pendulous from an adaxial placenta, the micropyle superior. Fruits firm-walled, few-seeded follicles completely dehiscent along the adaxial suture and apically on the abaxial suture. Seeds small, linear or oblong, tapered at each end; seed coat mem-

[4] Rank assigned by Cambessèdes, Monogr. *Spiraea*, 5. 1824.

branaceous, areolate-scalariform; endosperm absent or scarce; embryo elongate, the cotyledons oblong, the radicle superior. LECTOTYPE SPECIES: *S. salicifolia* L.; see P. A. Rydberg, N. Am. Fl. 22: 245. 1908. (Name from Greek *speiraia*, used by Theophrastus for a shrub [apparently privet, *Ligustrum vulgare*] and applied by Clusius, Tournefort, and Linnaeus to this rosaceous genus.) — SPIREA.

Largely restricted to the North Temperate Zone and widespread in North America, eastern Europe (absent in western and middle Europe), and Asia. Probably fewer than 50 species are currently recognized, although recent estimates range from 70 to 120 species. About ten indigenous and six or more naturalized species occur in North America; six (including one introduced) occur in our area. *Spiraea Hartwegiana* Rydberg (*S. parvifolia* Bentham non Raf.), endemic to the highlands of south-central Mexico, is quite different from other species of the genus, and its relationships are obscure.

Section SPIRAEA (*Spiraria* Seringe in DC.) (inflorescence an elongate panicle or raceme terminating a long shoot) is represented in our area by three species. *Spiraea tomentosa* L., hardhack or steeple bush, $2n = 24$, occurs in low, moist, open, usually infertile habitats with acidic soils such as bogs, low meadows, and woodland borders from Prince Edward Island, Nova Scotia, and New Brunswick to Ontario, Manitoba, Michigan, and Minnesota southward to the Carolinas, northern Georgia, Tennessee, southeastern Missouri, Arkansas, and Kansas. The characteristically abaxially densely tomentose leaves and large, spirelike inflorescences give most individuals of this species a striking appearance. The flowers have reflexed calyx lobes, lack nectar rings, and are usually rose colored, although a white-flowered form is known. Plants occurring inland with the flowers loosely clustered on the inflorescence branches have been segregated as var. *rosea* (Raf.) Fernald, but there is complete intergradation with the typical variety. *Spiraea subcanescens* Rydb., described from South Carolina, is evidently a spontaneous hybrid between *S. tomentosa* and *S. alba*. Artificial hybrids between *S. tomentosa* and the *S. Douglasii-S. Menziesii* group of western North America are known.

Spiraea alba DuRoi and *S. latifolia* (Aiton) Borkh., both commonly called meadowsweet, are distinguished from *S. tomentosa* by their nearly glabrous leaves, usually white flowers, spreading calyx lobes, and the presence of a prominent nectar ring at the base of the filaments. *Spiraea alba*, $2n = 36$, occurs in moist open habitats, primarily to the west of the Appalachian Mountains, from extreme northwestern Vermont, western New York and southern Quebec to Michigan and Alberta, south to western North Carolina, Missouri, and South Dakota. This species is set off from *S. latifolia* by its yellowish-brown, rather than reddish, stems; finely serrate and rather narrow leaves, instead of coarsely-toothed broader ones; thyrsoid, instead of open-pyramidal, inflorescences; and strongly pubescent, rather than mostly glabrous, inflorescence branches. Also preferring moist conditions, but occurring primarily in and east of the Appalachians, *S.*

latifolia (*S. alba* var. *latifolia* (Aiton) Ahles), $2n = 36$, ranges from Newfoundland to North Carolina. Low plants with dense, cylindric to ovoid inflorescences lacking elongate lower branches and occurring in subarctic and alpine regions from Newfoundland, southern Labrador, and the Ungava district, south to the New England mountains, have been distinguished as var. *septentrionalis* Fernald (*S. septentrionalis* (Fernald) Löve & Löve). This variety has also been reported from the Keweenaw Peninsula of Michigan and the mountains of northern Virginia. A chromosome number of $2n = 54$ is known from populations on Mt. Washington, New Hampshire, and Hawksbill Mountain, Page Co., Virginia. The voucher specimen from Virginia (*Baldwin 5601*, GH) is, however, quite different in appearance from northern plants of this variety. In a study of variation in *S. alba* and *S. latifolia*, Kugel concluded that the two represent distinct species that hybridize extensively, especially in the region between the Straits of Mackinac and Lake Abitibi, and introgress toward both extremes.

Spiraea salicifolia L., $2n = 36$, is a Eurasian member of this section reportedly escaping from cultivation in the eastern United States and differing from the very similar *S. alba* by its usually pink flowers and its leaves broadest below, rather than above, the middle. The variations found in *S. tomentosa*, *S. alba*, and *S. latifolia* are paralleled to some degree in *S. Douglasii* Hooker, $2n = 36$, of western North America, in its vars. *Douglasii*, *roseata* (Rydb.) C. L. Hitchc., and *Menziesii* (Hooker) Presl.

Section CALOSPIRA K. Koch (inflorescence a compound corymb terminating a long shoot) is represented in our area by two indigenous and one introduced species. *Spiraea virginiana* Britton is a rare species of rocky stream banks endemic to the mountains of West Virginia, western North Carolina, and eastern Tennessee. This distinctive species is a much-branched shrub with nearly entire, obovate leaves and glaucous pedicels and floral cups.

Spiraea betulifolia Pallas var. *corymbosa* (Raf.) Wenzig, $2n = 27, 36$, a low, often rhizomatous shrub with simple or seldom-branched erect stems, coarsely serrate, broadly ovate or elliptic leaves, and often pubescent pedicels, occurs along stream banks and in rocky places in the mountains from northern New Jersey and Pennsylvania to West Virginia, Kentucky, North Carolina, Alabama, and Georgia. Plants with larger, apically truncate leaves and pink flowers have been recognized as f. *Campii* Fosberg. Varietas *lucida* (Douglas ex Greene) C. L. Hitchcock (*S. lucida* Douglas ex Greene; *S. betulifolia* sensu Hultén), $2n = 36$, ranges from British Columbia and Saskatchewan, south to Oregon, Wyoming, and North Dakota, and var. *betulifolia* occurs in eastern Siberia, Kamchatka, northeastern China, and Japan. The affinities of these three taxa have long been known, although they are often recognized at ranks other than that of variety (see discussions in Fosberg, Greene, Hitchcock *et al.*, Hultén, and Komarov). Most characters used to distinguish the three such as indumentum density, sepals reflexed or erect in fruit, and the position of the stylar beak on the follicles, are too variable to be diagnostic. How-

ever, the North American varieties are rhizomatous (var. *lucida* more strongly so than var. *corymbosa*), and the plants usually are larger than those of var. *betulifolia*, the branches of which are said to arise from dense, globose crowns. *Spiraea Stevenii* (Schneider) Rydb. (*S. Beauverdiana* auct., non Schneider, see Uttal, Bull. Torrey Bot. Club 100: 236, 237. 1973), $2n = 18$, is evidently a closely related, but distinct, species distributed from eastern Siberia and Kamchatka to Alaska and the Yukon.

Spiraea japonica L. f., $2n = 18, 36$, characterized by long-acuminate and sharply serrate leaves and conspicuously pubescent pedicels and floral cups, is locally naturalized from New England to Georgia. Among other species assigned to sect. CALOSPIRA are *S. densiflora* Nutt. ex T. & G. (northwestern North America), $2n = 18$, *S. decumbens* Koch in Röhling (southeastern Alps), and *S. Baldschuanica* B. Fedtsch. (Central Asia); Rehder lists 17 additional species that are mostly of China and the Himalayas.

The twenty or more species of sect. CHAMAEDRYON Seringe in DC. (subg. *Nothospiraea* Zabel) (inflorescence a simple corymb or umbel terminating a short, lateral shoot or sessile on a long shoot) are native to central and eastern Europe and Asia. A number of them, including *Spiraea chamaedryfolia* L., $2n = 18, 36$, *S. prunifolia* Sieb. & Zucc., $2n = 18$, *S. Thunbergii* Sieb., and *S.* × *Vanhouttei* (Briot) Zabel, are commonly cultivated in the eastern States and sometimes persist afterward.

Tribe Spiraeeae, delimited by the usual absence of stipules and by free or basally united, antepetalous (when 5) carpels, wingless seeds, membranaceous seed coats, and the sparse development of endosperm, is composed of six genera: *Spiraea*, *Aruncus* L., *Petrophytum* (Nutt. ex T. & G.) Rydb. (three species of western North America), *Kelseya* (Watson) Rydb. (*K. uniflora* (Watson) Rydb., of Montana, Idaho, and Wyoming), *Luetkea* Bongard (*L. pectinata* (Pursh) Kuntze, of northwestern North America), and *Sibiraea* Maxim. (two to six species of northwestern Europe and Asia). *Apopetalum* Pax (one species of Bolivia), sometimes referred to this tribe, is a synonym of *Brunellia* Ruiz & Pavon, of the Brunelliaceae.

The basic taxonomic works on *Spiraea* are by Cambessèdes (1824), Maximowicz (1879), Zabel (1893), and Schneider (1905). All are quite out of date, and a modern revision using biosystematic, as well as classical, methodology is needed. Huber has recently indicated that the customary division of the genus into three sections does not show true infrageneric relationships, and he assigns the indigenous or naturalized species of Central Europe to nine species groups.

Reported sporophytic chromosome numbers in *Spiraea*, *sensu stricto*, are 10, 18, 27, 36, and 54, with a basic number of 9. All species of sect. SPIRAEA are tetraploid ($2n = 36$) except for the hexaploid *S. latifolia* var. *septentrionalis*. The Old World members of sect. CALOSPIRA are mostly diploids, while the New World species are predominantly tetraploids. Plants of *S. Stevenii* (eastern Russia) and the very closely related *S. densiflora* (northwestern North America) are diploid. Both diploid and

tetraploid plants are known in *S. japonica*. Sax reported a triploid cultivated plant of *S. betulifolia* var. *corymbosa*, and Baldwin found two tetraploid populations of this variety in Virginia. Most species of sect. CHAMAEDRYON are diploid, although *S. myrtilloides* Rehder is hexaploid, *S. chamaedryfolia* var. *ulmifolia* is tetraploid, and *S. media* has been reported as $2n = 10$ and 18.

Sterility barriers are not well developed in the genus, and artificial crosses have been made between both species belonging to different sections and species native to the Old and New worlds. Rehder (1940) listed hybrids involving all species in our area, except *S. virginiana*. Hybridization in nature, however, is infrequent, since the species are often geographically, ecologically, or phenologically isolated. Evidence has recently been presented by Hess that shows rather conclusively the hybrid origin of *S. pyramidata* Greene (*S. Douglasii* var. *Menziesii* × *S. betulifolia* var. *lucida*). As previously mentioned, *S. alba* and *S. latifolia* are thought to hybridize extensively toward the northern limits of their ranges.

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3. **Aruncus** Linnaeus, Opera Varia 259. 1758.[5]

Perennial herbs with several tall stems, largely unbranched below the inflorescence, arising from crowns on a thick, woody, branched rhizome; cortex fibrous with the vascular bundles forming a ± continuous, tough ring that surrounds a large, whitish, soft, spongy pith; indumentum of simple, recurved trichomes, variable in density. Leaves alternate, large, compound, irregularly ternate, imparibipinnate, or imparitripinnate, usually long petiolate, the petiolar bases half sheathing the stems; leaflets doubly serrate and sometimes lobed or subdivided, long petiolulate; stip-

[5] The generic name was published in the part of *Opera Varia* that is a reprint of the second edition of *Systema Naturae*, originally published in 1740. Although Linnaeus recognized *Aruncus* as a genus in his early publications, he considered it a synonym of *Spiraea* in all post-1753 works. In an analogous situation with *Dalea* L. (Leguminosae), Barneby (Taxon **14:** 163. 1965) argued that "the adoption by means of a pirated edition of an opinion which Linnaeus had roundly and repeatedly rejected in his mature judgment cannot be tolerated; or if tolerated it cannot be attributed to Linnaeus." However, such complications are unavoidable with an arbitrary starting point for botanical nomenclature, and it seems that we are obliged to attribute the name *Aruncus* to Linnaeus, since there is nothing in *Opera Varia* to indicate that he did not accept it.

FIGURE 2. **Aruncus.** a–k, *A. dioicus*: a, upper part of flowering stem, staminate plant, × 1/4; b, portion of rhizome with stem base, vegetative buds, and adventitious roots, × 1/2; c, carpellate flower — note rudimentary stamens, × 12; d, staminate flower, stamens not fully expanded, 3 stigmas of rudimentary carpels in center, × 12; e, staminate flower in vertical section to show nectar ring, rudimentary carpels, and insertion of stamens and petals, × 12; f, perfect flower from inflorescence of "staminate" plant in vertical section, not all stamens expanded, petals removed, × 12; g, portion of infructescence, showing reflexed fruits, × 5; h, developing fruit in section to show pendulous ovules, the micropyle superior, × 12; i, seed with loose, membranaceous seed coat, × 20; j, embryo, oriented as in "i," × 20; k, same, side view, × 20.

ules absent. Inflorescences of numerous racemes organized in large, terminal panicles, bracteate, each pedicel with a bracteole. Flowers white or greenish, quite small, imperfect or rarely perfect and the plants dioecious to polygamodioecious. Calyx lobes 5, short, triangular, spreading, persistent in fruit, valvate in aestivation; floral cup shallow, basin shaped. Petals 5, obovate to elliptic, narrowed or shortly clawed at the bases, the apices obtuse, imbricate or contorted, inserted at the edge of the floral cup. Staminate flowers with an androecium of usually 20 (15–30) exserted stamens; filaments slender, unequal in length, free, inserted in a single series at the edge of the floral cup between the calyx and a fleshy nectar ring that surrounds the mouth of the cup; anthers small; several vestigial carpels present. Carpellate flowers smaller, with a gynoecium of 3 (2–5, antepetalous when 5) free carpels; styles short, terminal, forming a beak on the fruit; stigmas capitate-discoid; each carpel with few anatropous ovules pendulous from an adaxial ventral placenta, the micropyle superior; rudimentary stamens present; nectar ring scarcely developed. Follicles as numerous as the carpels, shining, completely dehiscent along the adaxial suture and apically along the abaxial one, the pedicels recurving and inverting the fruits. Seeds 2–4, small, the seed coat loose, membranaceous, caudate at both ends, scalariform-reticulate; endosperm scanty; embryo spathulate. TYPE SPECIES: *Spiraea Aruncus* L. = *A. dioicus* (Walter) Fernald. (Latin name from Greek, *aryngos*, goat's beard, first used by Pliny; pre-Linnaean authors called the genus *Barba caprae*.) — GOAT'S BEARD.

A single polymorphic species disjunct in mountainous regions of the North Temperate and Subarctic zones, occuring in the eastern United States, Pacific North America, Alaska and the Aleutian Islands, central and eastern Europe, eastern Siberia to Kamchatka, eastern China, and Japan.

In eastern North America, *Aruncus dioicus* is found in or along the margins of rich woods, moist or rocky woodlands, bluffs, and ravines in mountainous or hilly terrain from Pennsylvania, west to Illinois, Iowa, and Missouri, and south to the Carolinas, northern Georgia, Alabama, Arkansas, and Oklahoma. In the eastern part of its range, most plants have rather lustrous foliage, glabrous or scarcely pubescent lower leaf surfaces and rather broad, ovoid follicles; these plants represent var. *dioicus* (*A. allegheniensis* Rydb.). Varietas *pubescens* (Rydb.) Fernald, with dull foliage, mostly pubescent lower leaf surfaces, and narrower, subcylindric follicles, is the predominant form in the Midwest, particularly in the Ozark Mountains, but such plants occur as far east as West Virginia. These two varieties intergrade completely, and it is questionable whether they should be maintained.

The variability within the genus is reflected by the number of segregate species that have been proposed. Rydberg recognized five in North America, and, in the Flora of the USSR, Pojarkova (see Komarov) distinguished four species. More recently, Hara (1955) and Tutin (1967)

have considered *Aruncus* to be composed of a single, polymorphic species, Hara recognizing thirteen varieties, one of which he subsequently elevated to subspecific status. Varietas *acuminatus* (Rydb.) Hara, ranging from northwestern California to Alaska and differing from vars. *dioicus* and *pubescens* by the shorter stylar beaks and larger follicles and seeds, is very similar to var. *vulgaris* (Raf. ex Maxim.) Hara (*A. vulgaris* Raf. ex Maxim.; *A. Aruncus* (L.) Karst.; *A. sylvester* Kostel., nom. nud.), of Central Europe.

In our area, *Aruncus dioicus* and *Astilbe biternata* (Saxifragaceae) are examples of convergent evolution, both species having a remarkably similar aspect and being especially alike in habit and leaf and inflorescence morphology. Both occur in the same habitats and can grow side by side, although *Astilbe biternata* has a more restricted range (Virginia and West Virginia to Georgia and Tennessee). This strong resemblance is superficial, however, and *Astilbe biternata* differs from *Aruncus dioicus* by its glandular, rather than simple, trichomes; ten, rather than twenty, stamens; two partly united, rather than three or four free, carpels; and many-seeded follicles about 4 mm. long, rather than two- to four-seeded follicles less than 2.5 mm. long. Like *Aruncus*, *Astilbe* is particularly variable in Asia, and over twenty species have been described from China, Japan, and the Himalayas. The degree of convergence between Asiatic species of *Astilbe* and varieties of *Aruncus dioicus* has not yet been studied.

The flowers of *Aruncus dioicus* are mostly functionally imperfect and the plants dioecious. Carpellate flowers have rudimentary stamens, while staminate flowers have vestigial carpels that occasionally develop fully in certain flowers of a staminate inflorescence and set fruit. Bond found that perfect flowers occur together in groups toward the apices of the racemes or that entire secondary panicles sometimes contain only perfect flowers. Seeds from fruit developing from perfect flowers give rise to staminate plants that always produce some perfect flowers. Observations on a living plant in the Arnold Arboretum indicate that plants with perfect flowers are self compatible. Thus far, perfect flowers are not known to occur in carpellate inflorescences. Hara reports that subsp. *triternatus* (Wall.) Hara, of the Himalayas, tends to have perfect flowers.

Reported chromosome numbers for *Aruncus* are $2n = 14$, 16, 18, 36, and 42, with 18 the most common. Polyploidy is evidently very infrequent. The only counts from North American plants (from British Columbia) are $2n = 18$.

Aruncus dioicus is commonly grown for its showy inflorescences (because of their larger flowers, staminate plants are the better suited for cultivation). The leaves and flowers have been used as fever-reducing agents. A cyanogenic glucoside is supposedly present in all parts of the plant.

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Tribe SORBARIEAE Rydberg

4. **Porteranthus** Britton, Mem. Torrey Bot. Club **4**: 115. *pls. 76, 77*. 1894.

Perennial herbs with one or more principal stems arising from woody horizontal rhizomes, lateral branches none or few below the inflorescence; roots with thick periderm, the larger ones often helical; indumentum of simple, glandular, and (on the sepals) stellate trichomes. Leaves alternate, trifoliolate or simple (in the inflorescence), sessile or shortly petiolate; leaflets subsessile, serrate with glandular-tipped teeth (leaflets of the lower leaves pinnately dentate or divided in *P. stipulatus*); stipules persistent, subulate or foliaceous and easily mistaken for 2 extra leaflets. Inflorescences terminal, loose, long-pedicellate, several-flowered panicles. Flowers white to pinkish, slightly irregular. Calyx ebracteolate, the 5 lobes erect, persistent, imbricate in aestivation; floral tube cylindric to slightly campanulate or urceolate, 10-nerved, free from the carpels, nectar ring not evident. Petals spreading somewhat, slightly unequal, linear to narrowly oblanceolate, clawed, deciduous, convolute in bud, perigynously inserted at the edge of the floral tube. Androecium of 20 (rarely more or

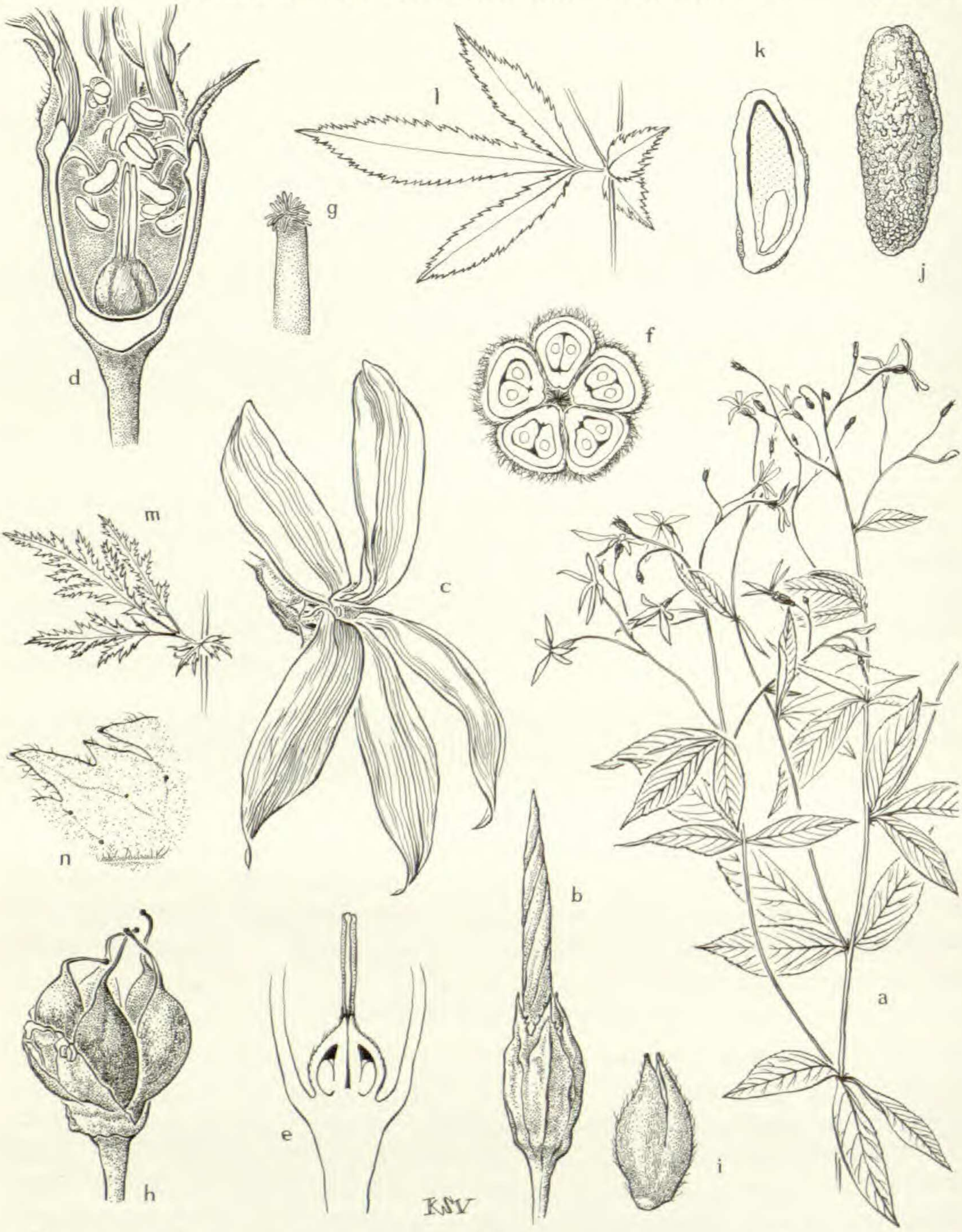

FIGURE 3. **Porteranthus.** a–k, *P. trifoliatus*: a, upper part of flowering plant — note small stipules, × 1/4; b, flower bud, petals contorted, × 3; c, flower, petal-arrangement somewhat zygomorphic by lateral displacement, × 2; d, slightly off-center vertical section of floral tube to show attachment of petals and stamens, × 5; e, base of floral cup and gynoecium in diagrammatic vertical section to show ovules, the micropyle inferior, × 6; f, gynoecium in semidiagrammatic cross section showing the 5 adpressed, but distinct, carpels, each with 2 ovules, × 12; g, tip of style with stigmatic papillae, × 25; h, mature, undehisced follicles, × 3; i, abaxial surface of an open follicle, abaxial suture partly split, × 3; j, seed, × 6; k, seed in vertical section, seed coat thick (white), endosperm abundant (stippled), embryo small (unshaded), × 6. l–n, *P. stipulatus*: l, leaf from near base of inflorescence, stipules foliaceous, × 1/2; m, leaf from near base of plant, × 1/2; n, detail of lower leaf surface — note both simple and glandular, sessile trichomes, × 10.

fewer) included or scarcely exserted stamens, ten in the upper whorl, 5 in the middle, antepetalous whorl, and 5 in the lower, antesepalous whorl; filaments short, incurved, free, perigynous on the floral tube; anthers rather large. Gynoecium superior, of 5 antesepalous carpels, ± connate at first, becoming distinct in fruit; styles terminal, punctiform; each carpel with 2–4 ascending anatropous ovules on a single adaxial and basal placenta, the micropyle inferior. Follicles rupturing the floral tube, 1 to few seeded, dehiscing completely on the adaxial suture and partially on the abaxial one. Seeds ovoid or ellipsoid, rugulose or verruculose, endosperm thick, fleshy; embryo spathulate, the cotyledons linear-oblong, flat, the radicle inferior. (*Gillenia* Moench, 1802, non *Gillena* Adanson, 1763).[6] TYPE SPECIES: *P. trifoliatus* (L.) Britton. (Name commemorating T. C. Porter, 1822–1901, botanist at Lafayette College.) — INDIAN PHYSIC.

Two very distinct species restricted to eastern North America, *Porteranthus trifoliatus* (*Gillenia trifoliata* (L.) Moench) and *P. stipulatus* (Muhl. ex Willd.) Britton (*G. stipulata* (Muhl. ex Willd.) Baillon; *Spiraea stipulacea* Pursh, sphalm).

Porteranthus trifoliatus, $2n = 18$, bowman's root, occurs primarily in the mountains and Upper Piedmont of the Appalachian mountain system from northern Alabama to western New York and southern Ontario at altitudes often above 3000 feet; the collections reported from Missouri by Steyermark (Fl. Missouri, 796) probably represent plants introduced along a railroad right-of-way. Characterized by small, linear stipules; sparse indumentum with glandular trichomes largely confined to leaflet dentation tips; monomorphic cauline leaves with leaflets of the lowermost slightly smaller and broader than the upper; pubescent, scarcely wrinkled, shortly beaked follicles; and ellipsoid seeds ca. 5 mm. long, *P. trifoliatus* is most frequently collected in rich woods, but also occurs in open, dry, rocky woods and along highway cuts. There are indications that this species prefers acidic soils.

Porteranthus stipulatus, American ipecac, usually occurs in dry, open upland woods, ranging from northeastern West Virginia, Ohio, Indiana, Illinois, and Missouri south to the Lower Piedmont of North Carolina, Louisiana, northeastern Texas, eastern Oklahoma, and southeastern Kansas. This species is distinguished by large foliaceous stipules that superficially resemble two extra leaflets; glandular trichomes abundant on the lower surfaces of the leaflets; dimorphic cauline leaves with the lowermost having pinnatifid leaflets; nearly glabrous, prominently wrinkled and veined, long-beaked follicles; and ovoid seeds ca. 3.5 mm. long. Rad-

[6] *Gillenia* Moench is a later homonym and an orthographic variant of *Gillena* Adanson (= *Clethra* L.), both names commemorating Arnold Gille (latinized as Gillenius), who, according to Stearn, was a medical man with a botanical garden at Kassel in 1627. It does not seem worthwhile to propose *Gillenia* Moench for conservation, since *Porteranthus* has been in limited use, the nomenclatural combinations have already been made, and there are only two species of limited geographical distribution and economic use.

ford *et al.* (Man. Vasc. Fl. Carolinas, 554) state that this species occurs primarily in basic soils in the Carolinas, while Steyermark (*loc. cit.*) indicates that it prefers acidic soils in Missouri.

Porteranthus; *Spiraeanthus Schrenckianus* (Fisch. & Mey.) Maxim., of central Asia; *Chamaebatiaria Millefolium* (Torrey) Maxim., of the western United States; and *Sorbaria* (Ser. in DC.) A. Braun, 10 to 15 spp. of temperate Asia, comprise the tribe Sorbarieae, which is characterized by persistent basally connate stipules, antesepalous carpels, and wingless seeds. Only *Porteranthus* is herbaceous; the other three genera are shrubs or subshrubs. *Porteranthus* (as *Gillenia*) and *Spiraeanthus* were segregated as tribe Gillenieae Maxim. by Schulze-Menz.

The red young stems and buds, white to pinkish flowers, reddish-brown fruits, and neat habit give plants of both species an attractive, though not spectacular, appearance, and they are grown to some extent as perennials and rock garden plants in the United States and Europe. The American Indians apparently used the rhizome of both species in medicinal preparations, particularly as an emetic.

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(*To be continued*)